Proof of principle: the adaptive geometry of social foragers

Marcus J. Dostie [a, b], David Lusseau [c], Tyler Bonnell [b, d], Parry M. R. Clarke [b], George Chaplin [e], Stefan Kienzle [a, b], Louise Barrett [b, d], S. Peter Henzi [b, d, *]

[a] Department of Geography, University of Lethbridge, Lethbridge, Canada
[b] Applied Behavioural Ecology and Ecosystems Research Unit, The University of South Africa, Florida, South Africa
[c] Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen, U.K.
[d] Department of Psychology, University of Lethbridge, Lethbridge, Canada
[e] Department of Anthropology, Pennsylvania State University, University Park, PA, U.S.A.

The spatial configuration of a group of animals should reflect the ability of its members to respond to environmental contingencies. Under predation risk, the optimal position for an individual in a stationary group is at the group's centre. The resulting group geometry is circular, with individual placement determined by competitive ability. Where it compromises efficient foraging, a long-standing question has been whether this topology can deform adaptively in response to the local distribution of resources. Here we show that the shape described by a group of foraging chacma baboons, *Papio hamadryas ursinus*, changes in response to habitat structure and that this promotes foraging efficiency while conserving the predation-risk-related distribution of group members. Adult baboons improve unimpeded access to the small, dispersed food items found in grassland by adjusting both their interindividual distances and their relative positions along the line of movement in order to forage in rank formation. Dominant animals occupy the centre of the group and do so regardless of its geometry. Our results demonstrate that spatially explicit data can address emergent group level properties directly. This global approach complements analyses of individual action and can help direct the search for potential local rules of interaction.

Principle Ten. A rank foraging formation will be favored whenever there is an advantage to remaining in a group and the group is foraging on slowly renewing resources that are of low overall density in the home range and are not locally abundant. (Altmann, 1974, p. 241)

The spatial configuration of a group of animals is the summation of the responses of its members to the local environment, made under the constraint of association (Parrish & Edelstein-Keshet, 1999). In mobile groups this emergent geometry is expected to deform adaptively as group members accommodate to local shifts in the relative salience of competing costs (Beecham & Farnsworth, 1999; Morrell, Ruxton, & James, 2011).

Social species, such as primates, that form groups to reduce the risk of predation for their members (Hill & Dunbar, 1998; Shultz, Opie, & Atkinson, 2012) do so at the expense of increasing local competition for resources (Majolo, de Bortoli Vizioli, & Schino, 2008; van Schaik, 1983). Heterogeneity in the distribution of these risks and costs both among group members (Koenig, 2002; Ron, Henzi, & Motro, 1996) and across the landscape (Willems & Hill, 2009), makes such groups well suited to investigating the environmental drivers of the spatial structure of social units (Krause & Ruxton, 2002; Morrell et al., 2011).

Under marginal predation, where animals on the edge of groups are more vulnerable to predators, those that are closer to the group's centre have smaller domains of danger and are less exposed to risk (Hamilton, 1971; King et al., 2012; Morrell & Romey, 2008). Local adjustments in response to risk perception will then generate a group geometry that ideally, in two dimensions, is circular (Aurenhammer, 1991), with individual location determined by resource-holding potential (Parker, 1974), which can be indexed as dominance rank. This configuration is likely to characterize the global structure of animal groups primarily where high-quality resources are clumped and can be defended, and marginal animals can balance increased predation risk against the possibility of improved foraging opportunities offered by a reduction in contest competition (Bumann, Krause, & Rubenstein, 1997; Krause &

* Correspondence: S. P. Henzi, Department of Psychology, University of Lethbridge, 4401 University Drive, Lethbridge T1K 3M4, Canada.
E-mail address: peter.henzi@uleth.ca (S. P. Henzi).

Ruxton, 2002; Robinson, 1981). The question, then, is whether the accommodation of this 'selfish herd' (Hamilton, 1971) to changing cost potentials (Beecham & Farnsworth, 1999) can be detected at the global level as a change in adaptive topology?

Savannah baboons, *Papio hamadryas*, have home ranges that encompass habitat mosaics and frequently forage in grasslands (Henzi & Barrett, 2005), which are typified by low-quality, thinly dispersed, quickly consumed foods (Henzi, Byrne, & Whiten, 1992). These induce scramble competition (Isbell, 1991), where the persistence of a circular formation would reduce foraging efficiency for all but those animals in the group's vanguard (Hirsch, 2007). Altmann (1974) instantiated and extended Hamilton's (1971) general theoretical argument to predict that in grassland, where ephemeral resources are thinly distributed, group members will spread out to secure at least the minimum foraging swath that enables unimpeded foraging while adjusting their positions to keep abreast of their neighbours and thereby minimize the costs of scramble competition. The geometry of this foraging group is expected, therefore, to deform to a rank formation as animals encounter low-quality, dispersed resources, while the spread of the group will be constrained by continuing predation risk. As an implicit but necessary corollary, we also expect more dominant animals to continue to avoid the margins of the group as the shape shifts.

An assessment of these long-standing propositions can contribute to the development of a coherent group level spatial ecology that complements current research on individual contributions to collective movement (Katz, Tunstrøm, Ioannou, Huepe, & Couzin, 2011; Nagy, Ákos, Biro, & Vicsek, 2010; Parrish & Edelstein-Keshet, 1999; Strandburg-Peshkin, Farine, Couzin, & Crofoot, 2015; Sumpter, Mann, & Perna, 2012), but has had to wait on the emergence of appropriate global positioning system (GPS) technologies and geospatial analytics (Tomkiewicz, Fuller, Kie, & Bates, 2010). Here, we use interpolated GPS data collected from individual adults to describe dynamic spatial relationships in a group of chacma baboons, *Papio hamadryas ursinus*, as it moves through its home range, which comprises a mix of open grassland and dense scrub (Kotze & Fairall, 2006).

METHODS

Study Site and Data Collection

We collected 74 days of data, spread across 391 days, from a habituated group of chacma baboons ($N \approx 45$) at De Hoop Nature Reserve, South Africa (Barrett, Gaynor, Rendall, Mitchell, & Henzi, 2004) during 2007 and early 2008. A single observer, using a handheld GPS-equipped data logger followed and recorded the spatial locations of all 14 adult members (three males, 11 females). On-site calibration of the data loggers confirmed that they were absolutely accurate to within 2–5 m and relatively accurate to ca. 1 m (viz. the accuracy with which the distance between two points can be estimated). Beginning at one end of the group, the observer identified, stood next to and collected a GPS record for each visible adult in turn. When the distal end of the group was reached, the observer turned back along the line of travel while continuing to collect data. If an animal was not seen during two circuits of the troop, the observer interrupted data collection in order to locate it. We obtained 61 842 usable data points, with a mean of 63.98 points (±9.03 SD)/individual per day. Foraging effort was determined from scan sample records of activity ($N = 5846$), collected as standard procedure (Henzi, Lusseau, Weingrill, Schaik, & Barrett, 2009) every 30 min from all visible, identified individuals, and expressed as the proportion of the group foraging. Animals were assigned an ordinal dominance rank derived from ad libitum records of all dyadic

agonistic interactions over the study period, with participants identified as winners or losers. We used the Domicalc program (Schmid and de Vries, 2013) in R 3.2.1. (R Core Team, 2015) to confirm a high degree of linearity in the hierarchy ($h^1 = 1$, $N = 704$, $P < 0.0001$). All procedures were approved by the University of Lethbridge Animal Welfare Committee (Protocol #0702).

Interpolation and Estimates of Minimal Optimal Spread

While our spatial data collection procedure did not allow the simultaneous recording of all individual locations, the median time interval of 7 min between consecutive records for the same individual preserves sufficient information for analyses derived from individual points (Andrienko, Andrienko, Barrett, Dostie, & Henzi, 2013; Bonnell et al, in press), giving us confidence in the use of interpolated data. We therefore estimated the positions of all group members for any given time using linear interpolation of trajectories between successive point samples. To confirm that our baboons were sensitive to both predation risk and foraging interference, we followed the approach detailed in Aureli, Schaffner, Asensio, and Lusseau (2012), extracting the interindividual distances (IIDs, $N = 5204$, range 0–615 m) of all animals at 1100 hours each day, when animals were consistently likely to be foraging, and fitting them to three models, with model selection based on the Akaike information criterion (AIC). These models were derived from the relative ability of (1) food distribution and predation risk (the Ecological model), (2) foraging interference (the Biosocial model) or (3) both (the Socioecological model) to predict observed IIDs. In summary, the Ecological model is an integrated estimate of the spatial distribution of important ecological factors (predation risk, food) in the habitat, with individual distribution following a Poisson process in response to this background heterogeneity. The Biosocial model assumes that individual distribution is governed solely by repulsion from others at close distances and attraction towards them at intermediate distances. The Socioecological model, therefore, is an extension of the Biosocial model that accounts explicitly for the ecological landscape (see Aureli et al., 2012 for detail and derivations) in predicting individual distributions. It should be noted that, for these analyses, we make the simplifying assumption that the extracted distances of repulsion and attraction do not vary significantly across habitats and individual group members.

The Socioecological model provided the best fit to the data and consequently we doubled its estimate of the mean distance at which animals repelled one another to set the width of the swaths within which each animal might forage without interference. The degree to which individual swaths overlapped, estimated as a proportion of the distance along the x-axis (Fig. 1), constituted our group level estimate of the extent to which group spread reflected the predicted minimal requirements for unimpeded individual foraging in open country. The lower the overlap in foraging swaths, the more optimally the group was foraging. Where there was overlap in foraging swaths, we distinguished between animals in front (no immediate scramble competition) from those further back, who might be expected to encounter less food as a consequence of foraging in another animal's path.

Data Location Error and Temporal Independence

We constrained the data set to periods for which the average location error was predicted to be at or below 7.8 m, using a model of interpolation error derived from separately collected continuous tracks of individual baboons (Dostie, Bonnell, Barrett & Henzi, n.d.). This model estimated interpolation error by repeated subsampling of the continuous data and comparing the interpolated data